Zoosyst. Evol. 94 (2) 2018, 247–261 | DOI 10.3897/zse.94.21037

PENSOFT

für Natur MUSEUM FÜR NATURKUNDE BERLIN

A distinctive new frog species (Anura, Mantellidae) supports the biogeographic linkage of two montane rainforest massifs in northern Madagascar

Mark D. Scherz[1,2], Oliver Hawlitschek[2], Jary H. Razafindraibe[3], Steven Megson[4], Fanomezana Mihaja Ratsoavina[3], Andolalao Rakotoarison[2,3], Molly C. Bletz[2,5], Frank Glaw[1], Miguel Vences[2]

1 *Zoologische Staatssammlung München (ZSM-SNSB), Münchhausenstr. 21, 81247 Munich, Germany*
2 *Zoologisches Institut, Technische Universität Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany*
3 *Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar*
4 *School of Science and the Environment, Manchester Metropolitan University, Manchester, M1 5GD, UK*
5 *Department of Biology, University of Massachusetts Boston, 100 Morrissey Boulevard, Boston, MA 02125, USA*

http://zoobank.org/8A83DE58-A2EE-494F-A03C-820DC836CDDF

Corresponding author: *Mark D. Scherz* (mark.scherz@gmail.com)

Received 16 September 2017
Accepted 26 February 2018
Published 15 March 2018

Academic editor:
Johannes Penner

Key Words

Bioacoustics
Biogeography
Marojejy
Montane Endemism
Sorata
Taxonomy

Abstract

We describe a new species of the genus *Gephyromantis*, subgenus *Vatomantis* (Mantellidae, Mantellinae), from moderately high elevation (1164–1394 m a.s.l.) on the Marojejy, Sorata, and Andravory Massifs in northern Madagascar. The new species, *Gephyromantis* (*Vatomantis*) *lomorina* **sp. n.** is highly distinct from all other species, and was immediately recognisable as an undescribed taxon upon its discovery. It is characterised by a granular, mottled black and green skin, reddish eyes, paired subgular vocal sacs of partly white colour, bulbous femoral glands present only in males and consisting of three large granules, white ventral spotting, and a unique, amplitude-modulated advertisement call consisting of a series of 24–29 rapid, quiet notes at a dominant frequency of 5124–5512 Hz. Genetically the species is also strongly distinct from its congeners, with uncorrected pairwise distances ≥10 % in a fragment of the mitochondrial 16S rRNA gene to all other nominal *Gephyromantis* species. A molecular phylogeny based on 16S sequences places it in a clade with species of the subgenera *Laurentomantis* and *Vatomantis*, and we assign it to the latter subgenus based on its morphological resemblance to members of *Vatomantis*. We discuss the biogeography of reptiles and amphibians across the massifs of northern Madagascar, the evidence for a strong link between Marojejy and Sorata, and the role of elevation in determining community sharing across this landscape.

Introduction

In recent decades, the number of frog species that have been discovered in Madagascar, while steadily increasing (Köhler et al. 2005), often included species that were not immediately recognizable as new to science, though with occasional exceptions, e.g. *Boophis lichenoides* (Vallan et al. 1998), *Scaphiophryne boribory* (Vences et al. 2003), and *Tsingymantis antitra* (Glaw et al. 2006). The majority of newly discovered taxa are assignable to existing complexes and must be investigated closely before it can be confirmed whether or not they constitute new species (e.g. Vieites et al. 2012). Differing from this general pattern, on a 2012 expedition to the Sorata massif in northern Madagascar, we discovered a small green frog of the genus *Gephyromantis* that was immediately recognisable as a new species. It was not given a candidate species number at the time, and no sequences of this species were included in the barcoding assessment of Perl et al. (2014). In a 2016 survey in Andravory, near Sorata, and a 2016 survey of Marojejy National Park in northeastern Madagascar, we encountered the same species.

At present, 44 species of *Gephyromantis* are recognized and assigned to six subgenera (*Asperomantis*, *Duboimantis*, *Gephyromantis*, *Laurentomantis*, *Phylacomantis*, and *Vatomantis*) based on molecular and morphological criteria (Glaw and Vences 2006, Vences et al. 2017). This classification is largely in agreement with the molecular multi-gene phylogeny of Kaffenberger et al. (2012). However, this phylogenetic study revealed that the subgenera *Laurentomantis* and *Vatomantis* are closely related, and that *Gephyromantis klemmeri* Guibé, 1974, morphologically similar to other species of the subgenus *Gephyromantis*, is sister to the *Laurentomantis* clade, suggesting the need for an improved classification. We here provide a description of the new species, which has potential implications for the supraspecific taxonomy of *Gephyromantis*, and the biogeographical linkage of the rainforest massifs of northern Madagascar.

Materials and methods

Specimen collection and morphological measurement

Specimens were collected at night using head torches along montane streams, euthanized using MS222 anaesthesia and subsequent overdose, fixed in 96 % ethanol, and deposited in 75 % ethanol for long-term storage. Tissue samples were stored in 96 % ethanol. Field numbers refer to the zoological collections of Miguel Vences (ZCMV), Frank Glaw (FGZC), and Steven Megson (SM). Specimens were deposited in the amphibian collections of the Mention Zoologie et Biodiversité Animale, Université d'Antananarivo (UADBA-A) and the Zoologische Staatssammlung München (ZSM).

Morphological measurements were taken to the nearest 0.1 mm using a digital calliper. Measurement schemes followed generally previous work on the genus (e.g. Vences et al. 2017) with modifications to decrease the risk of damaging the fragile limbs of the specimens when ascertaining limb lengths: snout–vent length (SVL), maximum head width (HW), head length from posterior edge of tympanum to snout tip (HL), horizontal eye diameter (ED), horizontal tympanum diameter (TD), distance from eye to nostril (END), distance from nostril to snout tip (NSD), distance between nostrils (NND), upper arm length from the articulation of the arm with the trunk to the elbow (UAL), lower arm length from the elbow to the base of the hand (LAL), hand length from the base of the hand to the tip of the longest finger (HAL), forelimb length (FORL*, given by the sum of UAL, LAL, and HAL), forearm length (FARL, given by the sum of LAL and HAL), thigh length from cloaca to knee (THIL), tibia length from knee to heel (TIBL), tarsus length from heel to base of foot (TARL), foot length from base of foot to tip of longest toe (FOL), hindlimb length (HIL*, given by the sum of THIL, TIBL, TARL and FOL), and length and width of femoral gland (FGL, FGW). Asterisks in this list indicate measurements that have the same abbreviation as the analogous single-measurement of previous studies (e.g. Vences et al. 2017) but are cumulative here and therefore not necessarily equivalent; comparison of such values must be done cautiously.

Sequencing and analysis of DNA sequences

DNA was extracted from tissue samples using a Qiagen DNeasy blood & tissue kit (Qiagen, Hilden, Germany), or standard salt extraction protocols. For two samples from Sorata and one sample from Marojejy (ZCMV 15269), we amplified a fragment of the mitochondrial 16S rRNA gene (hereafter 16S) in 25 µl polymerase chain reactions with the primers 16Sra-L and 16Sb-H (Palumbi et al. 1991), 1 µl of template DNA, and the following steps: initial denaturation for 3 min at 94 °C, followed by denaturation with 35 cycles of 30 sec each at 94 °C, 30 sec of annealing at 55°C and 60 sec of elongation at 72 °C, and a final elongation step of 10 min at 72 °C. Sequencing was conducted using the BigDye Terminator v1.1 Cycle Sequencing Kit on ABI 3730 and ABI 3130xl capillary sequencers. Newly determined sequences were deposited in GenBank (accession numbers MG926811–MG926823). For an additional nine specimens from Marojejy, we sequenced a shorter, highly variable stretch of 250 bp of the same 16S region by an Illumina amplicon approach (Vences et al. 2016) to confirm their identification (data not shown).

For an exploratory analysis, we aligned the new sequences with 16S sequences used by Kaffenberger et al. (2012) for all nominal species of *Gephyromantis*. Because the obtained tree (not shown) confirmed the new species to be related to the *Laurentomantis/Vatomantis* clade as also strongly suggested by morphology, we focused our analysis on this subgroup, i.e., all nominal species of the subgenera *Laurentomantis* and *Vatomantis, a*nd *G. klemmeri* which is known to be related to these subgenera (Kaffenberger et al. 2012), as well as *G. granulatus* (subgenus *Duboimantis*) as outgroup.

We aligned sequences in MEGA 7 (Kumar et al. 2016), yielding an alignment of 532 positions of the sequenced stretch of the 16S rRNA gene. As only a few indels were found in this alignment, we did not exclude any positions for further analysis. We used the Bayesian Information Criterion in jModelTest 2.1.4 (Darriba et al. 2012) to determine a SYM+G substitution model as best-fitting our data. We implemented this model in MrBayes 3.2 (Ronquist et al. 2012) and computed a Bayesian inference phylogenetic analysis, with two independent runs of 20 million generations, each comprising four Markov Chains (three heated and one cold), sampling every 1000 generations. Chain mixing and stationarity were assessed by examining the standard deviation of split frequencies and by plotting the -lnL per generation using Tracer 1.5 software (Rambaut and Drummond 2007). Results were combined to obtain a 50 %-majority rule consensus tree and the respective posterior probabilities of nodes, after discarding 25 % of the generations as burn-in (all compatible nodes with probabilities <0.5 kept). In addition, we computed a Maximum Likelihood (ML) tree in MEGA 7, with a GTR+G model (as the SYM model is not available

in this program), SPR level 5 branch swapping, and 500 nonparametric bootstrap replicates. Genetic distances (uncorrected pairwise p-distances) were also calculated in MEGA 7.

Bioacoustic analyses

Recordings from Marojejy were made on a Marantz PMD661 MKII with a Sennheiser ME66/K6 supercardioid microphone, at a bandwidth of 44.1 kHz. Recordings from Sorata were made on an Edirol R-09 with its internal microphone. Call analysis was conducted in Cooledit 2.0 (Syntrillium Corp.). To obtain frequency information, the recording was transformed with Fast Fourier Transformation (FFT; width 1024 points). Spectrograms were created with a Hanning window of 512 or 256 bands. Measurements are given as mean ± one standard deviation, with range in parentheses. Terminology follows the recently-published recommendations of Köhler et al. (2017) with a note-centred approach. This definition is different from that of Vences et al. (2002) for *Laurentomantis* and Sabino-Pinto et al. (2014) for *Vatomantis*; the 'pulses' of those studies are here treated as notes, because each of these units in the new species described herein are distinctly pulsed, and therefore are treated as individual notes following Köhler et al. (2017). Recordings are deposited in the Animal Sound Archive of the Museum für Naturkunde, Berlin (DOI: 10.7479/nmx8-aq7v), and are available as Suppl. materials 1–2.

Taxonomic work

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is urn:lsid:zoobank.org:pub:8A83DE58-A2EE-494F-A03C-820DC836CDDF. The online version of this work will be archived and made available from the following digital repositories: CLOCKSS and Zenodo.

Results

Based on 16S sequences, the newly collected specimens represent an undescribed and hitherto unknown species of *Gephyromantis* that is highly distinct from all others (≥10 % p-distance). Exploratory phylogenetic analyses including all species of *Gephyromantis* clearly suggested their relationships with the subgenera *Laurentomantis* and *Vatomantis*, which also is strongly supported by morphological affinities, in particular by the greenish dorsal colour, granular skin, riparian habits, and paired subgular vocal sacs of partly white colour in males (see Diagnosis below for more details). A phylogenetic analysis of 16S sequences (total alignment length 532 bp) for all described species of *Laurentomantis* and *Vatomantis* as well as *G. klemmeri*, which was related to these subgenera in the multi-gene analysis of Kaffenberger et al. (2012), places the newly collected specimens sister to a clade with all described species of *Vatomantis*. *Gephyromantis klemmeri* is placed sister to *Laurentomantis*, although these basal nodes did not receive relevant support from ML bootstrap values or Bayesian posterior probabilities (Fig. 1). Genetic distances of the new specimens to all other species were high: 10.9–15.4 % to the three described species of *Vatomantis*, 10.0–13.2 % to species of *Laurentomantis*, and 12.2–12.5 % to *G. klemmeri.* The newly collected specimens from Sorata and Marojejy differed by 2.9 %, while no sequence differences were detected within each of these two localities, except for two mutations observed in one Marojejy specimen (ZCMV 15219).

Phenotypically the new specimens bear resemblance to both *Laurentomantis* and *Vatomantis*. Their advertisement call is more similar to *Laurentomantis*, but their morphological resemblance to *Vatomantis* is greater (see the diagnosis below). We here tentatively assign them to *Vatomantis* due to their morphological affinities and preliminary phylogenetic relationships. Given their very high genetic divergence to all other *Gephyromantis*, isolated phylogenetic position (not placed as close sister group to any other species), and morphological and bioacoustic differences, there is no doubt that these specimens belong to a new species, which we describe below.

Gephyromantis (*Vatomantis*) *lomorina* sp. n.

http://zoobank.org/5D2109C8-AD0A-434D-816F-51722FE7DCD7
Figs 1–4, Table 1, Suppl. materials 1–2

Holotype. ZSM 419/2016 (ZCMV 15221), adult male, collected at 21h20 on 18 November 2016 near Camp Simpona (ca. 14.4366°S, ca. 49.7434°E, ca. 1325 m a.s.l.) in Marojejy National Park, Sava Region, northeastern Madagascar, by M. D. Scherz, J. H. Razafindraibe, M. C. Bletz, A. Rakotoarison, A. Razafimanantsoa, and M. Vences (Fig. 2).

Paratypes. ZSM 418/2016 (ZCMV 15220), female, and ZSM 420–421/2016 (ZCMV 15222 and 15271), two males, collected between 17 and 19 November 2016 from the same locality and by the same collectors as the holotype; UADBA-A 60294–60299 (ZCMV 15219, 15223, 15247, 15270, 15272, and 15273), one male, three females, a subadult and an unsexed adult, collected between 17 and 19 November 2016 from the same locality and by the same collectors as the holotype; ZSM 1549/2012 (FGZC 3714), adult male, collected on 30 November 2012 in a creek near the campsite on the Sorata massif (13.6829°S, 49.4403°E, 1325 m a.s.l.), Sava Region, northeastern Madagascar,

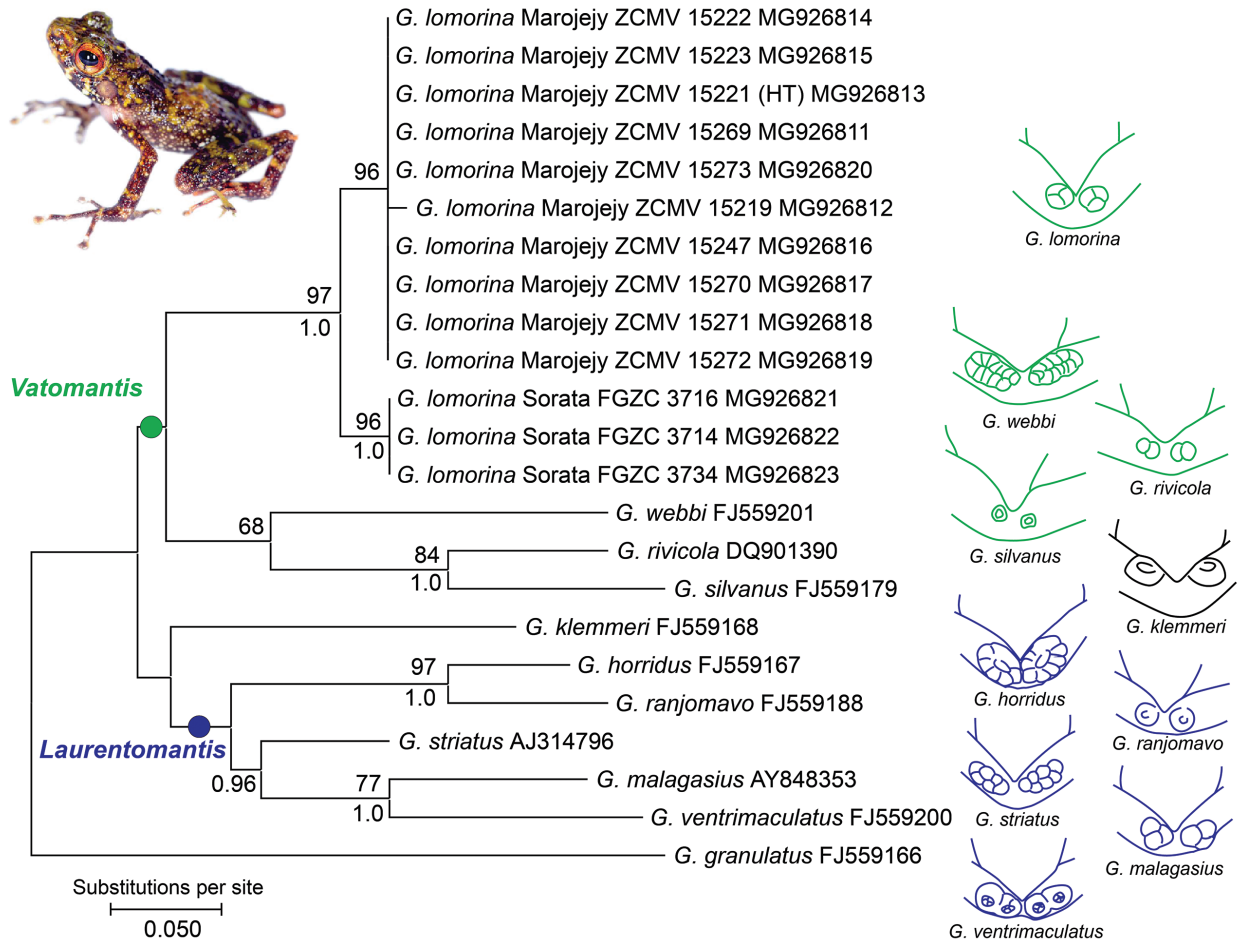

Figure 1. Preliminary phylogenetic tree of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n., based on Maximum Likelihood analysis of a 532 bp fragment of the mitochondrial 16S rRNA gene. Numbers at nodes indicate bootstrap values in percent (500 replicates, above) and posterior probabilities from a Bayesian Inference analysis (20 million generations, below), shown only if >50 % (bootstrap) or >90 % (posterior probabilities). Each specimen/species is followed by the corresponding GenBank accession number used in the alignment. Schematic drawings of femoral glands of all species in the subgenera *Laurentomantis* and *Vatomantis* as well as of *G. klemmeri* are shown to the right of the phylogeny, and coloured according to the subgenus to which they are assigned.

by O. Hawlitschek, F. Glaw, A. Rakotoarison, F. M. Ratsoavina, T. Rajoafiarison, and A. Razafimanantsoa; ZSM 1545–1547/2012 (FGZC 3716, 3734, and 3664), adult males, and ZSM 1548/2012 (FGZC 3721), adult female, collected between 28 and 30 November 2012 from a creek below a bamboo forest on the Sorata massif (13.6772°S, 49.4413°E, 1394 m above sea level), Sava Region, northeastern Madagascar, by O. Hawlitschek, F. Glaw, A. Rakotoarison, F. M. Ratsoavina, T. Rajoafiarison, and A. Razafimanantsoa; ZSM 318/2016 (SM AEA 063), adult female, and UADBA-A uncatalogued (SM AEA 062), unsexed adult, collected between 18h45 and 18h50 on 30 May 2016 in Andravory (13.7385–13.7388°S, 49.5310°E, 1164–1179 m a.s.l.), Sava Region, Antsiranana Province, northeastern Madagascar, by S. Megson, R. Walker, W.-Y. Crawley, and T. H. Rafeliarisoa (Figs 3–4).

Diagnosis. A species assigned to the genus *Gephyromantis* on the basis of its granular skin, moderately enlarged finger tips, small femoral glands consisting of a small number of large granules and present in males only (thus of type 2 as defined by Glaw et al. 2000), and bifid tongue. Within the genus *Gephyromantis*, assigned to the subgenus *Vatomantis* on the basis of its small size, connected lateral metatarsalia, absence of an outer metatarsal tubercle, paired subgular vocal sacs of partly whitish colour, greenish skin colouration, and riparian ecology. *Gephyromantis lomorina* sp. n. is characterized by the possession of the following suite of morphological characters: (1) granular skin, (2) reddish eyes, (3) mottled green and black skin, (4) males with paired subgular vocal sacs of partly white colour, (5) males with bulbous type 2 femoral glands consisting of a small number (2–3) of large granules, (6) white spots on the venter, (7) SVL 20.2–25.5 mm, and (8) fourth finger much longer than second. Furthermore, the species is characterised by distinctive, 1681–1827 ms advertisement calls of relatively low intensity, consisting of 24–30 individual pulsed notes,

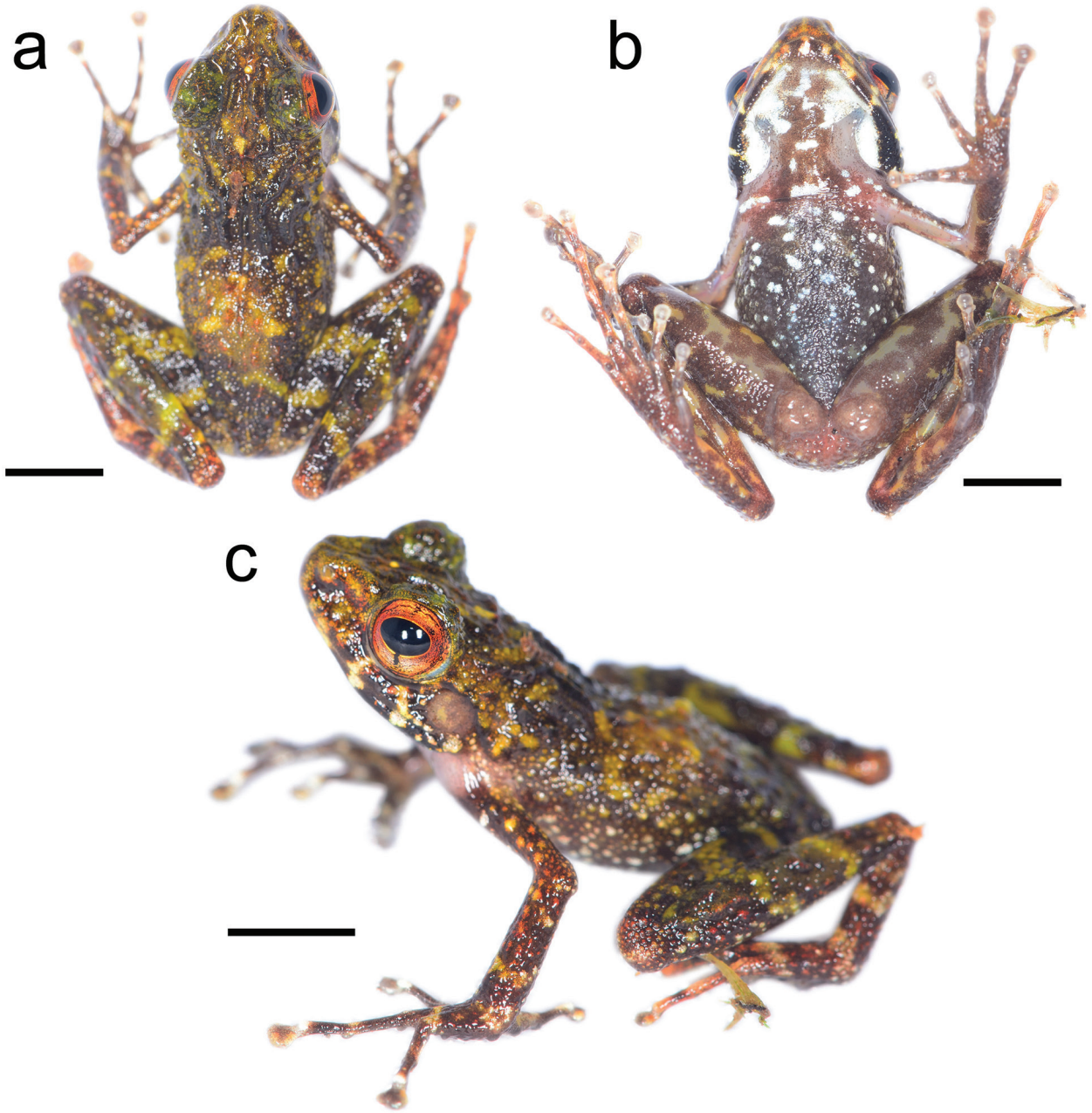

Figure 2. The holotype of *Gephyromantis lomorina* sp. n., ZSM 419/2016 (ZCMV 15221) in life. **(a)** Dorsal; **(b)** ventral; and **(c)** dorsolateral view. Scale bars indicate 5 mm.

with 2–4 pulses per note, an inter-note interval of 41–75 ms, and a dominant frequency of 5124–5555 Hz. DNA sequence data from the 16S gene fragment supports the high divergence of this taxon to all other *Gephyromantis*, and is in agreement with its subgeneric assignment, albeit without statistical support (Fig. 1).

Within the genus *Gephyromantis*, *G. lomorina* sp. n. can be distinguished from all subgenera except *Laurentomantis* and *Vatomantis* on the basis of the combination of femoral glands composed of few large granules (vs. composed of many, small granules; note that *G. klemmeri* is here treated separately from all other subgenera, below, due to its unclear assignment), SVL < 26 mm (vs. > 27 mm in all other subgenera except *Gephyromantis*), absence of a white stripe along the upper lip (vs. general presence in subgenus *Gephyromantis*), and absence of distinctly enlarged supraocular spines (vs. presence in *Asperomantis* and some *Duboimantis*). It may be distinguished from all members of the subgenus *Laurentomantis* (*G. ventrimaculatus* (Angel), *G. malagasius* (Methuen & Hewitt), *G. striatus* (Vences, Glaw, Andreone, Jesu & Schimmenti), *G. horridus* (Boettger), and *G. ranjomavo* Glaw & Vences) by paired subgular vocal sacs (vs. single), absence of outer metatarsal tubercles (vs. presence), and at least partly greenish dorsal skin (vs. mostly yellowish to brown to reddish), and from several of these by the

Table 1. Morphological data on specimens of *Gephyromantis lomorina* sp. n. Abbreviations: m = male, f = female, sa = subadult; for measurement abbreviations, see the Materials and methods. The holotype is bolded. Additive measurements (FARL, FORL, and HIL) are not explicitly shown but can be deduced from these data.

Catalogue (field number)	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	UAL	LAL	HAL	THIL	TIBL	TARL	FOL	FGL	FGW
ZSM 419/2016 (ZCMV 15221)	**m**	**23.3**	**7.2**	**8.5**	**2.1**	**4.0**	**2.2**	**1.4**	**2.2**	**6.0**	**7.3**	**8.2**	**13.4**	**13.9**	**7.4**	**12.1**	**2.8**	**2.0**
ZSM 421/2016 (ZCMV 15271)	m	22.2	6.6	8.2	1.9	3.4	2.1	1.5	2.2	4.8	6.0	8.0	12.2	12.8	7.0	10.6	2.2	1.8
ZSM 420/2016 (ZCMV 15222)	m	23.0	7.3	9.1	1.9	3.0	1.9	1.5	2.1	5.1	6.8	8.2	11.5	13.3	7.0	11.8	2.2	1.5
ZSM 418/2016 (ZCMV 15220)	f	25.5	7.7	9.1	2.0	4.1	2.4	1.4	2.1	5.2	7.7	8.4	13.6	14.8	6.7	12.6	n/a	n/a
UADBA·A 60294 (ZCMV 15270)	m	22.1	6.5	8.0	2.7	3.4	1.5	1.4	1.9	4.9	6.1	7.2	10.8	12.3	6.4	11.0	2.6	1.6
UADBA·A 60298 (ZCMV 15273)	f	24.6	7.6	9.0	2.0	3.8	2.2	1.4	2.1	6.4	6.4	8.3	12.1	13.5	7.3	12.4	n/a	n/a
UADBA·A 60296 (ZCMV 15223)	sa	20.2	5.7	7.8	1.6	3.1	1.9	1.6	1.9	4.8	5.9	7.6	11.1	12.0	6.6	9.5	n/a	n/a
UADBA·A 60297 (ZCMV 15272)	f	24.6	8.0	8.7	2.1	3.5	2.4	1.3	2.2	5.7	6.1	8.6	12.4	14.7	7.3	12.0	n/a	n/a
UADBA·A 60295 (ZCMV 15219)	f	23.2	6.8	8.5	2.0	3.6	2.0	1.4	2.0	5.6	6.9	8.1	12.6	14.9	7.6	11.6	n/a	n/a
UADBA·A 60299 (ZCMV 15247)	f	22.0	7.0	8.1	2.1	3.5	2.3	1.5	2.0	5.0	6.0	7.5	10.4	12.4	7.0	11.6	n/a	n/a
ZSM 1549/2012 (FGZC 3714)	m	23.3	8.0	8.3	2.3	3.3	2.6	1.5	1.9	5.8	6.7	8.8	11.1	13.2	6.7	12.6	3.0	2.1
ZSM 1545/2012 (FGZC 3716)	m	22.8	7.1	8.0	2.2	3.0	2.8	1.5	2.1	6.0	6.9	8.1	11.9	13.1	6.7	13.2	2.9	2.1
ZSM 1546/2012 (FGZC 3734)	m	24.6	8.0	9.7	2.2	3.3	2.8	1.6	2.3	7.0	7.5	9.3	13.1	14.5	6.6	13.4	3.4	2.5
ZSM 1547/2012 (FGZC 3664)	m	23.9	8.1	9.1	2.2	3.4	2.6	1.6	2.2	6.4	7.0	9.5	12.1	14.2	6.5	13.6	2.5	2.1
ZSM 1548/2012 (FGZC 3721)	f	24.1	7.7	9.2	2.2	2.8	2.8	1.4	2.2	5.5	6.6	9.3	12.5	14.0	6.5	13.8	n/a	n/a
ZSM 318/2016 (SM AEA 063)	f	25.2	7.9	9.4	2.1	2.6	3.0	2.0	2.4	7.1	6.4	8.9	13.6	14.2	7.2	13.6	n/a	n/a

absence of tibial glands in males (vs. typical presence). Within the subgenus *Vatomantis*, *G. lomorina* sp. n. may be distinguished from all species by its more granular dorsal skin (vs. granular but not rough) and venter spotted with white (vs. generally without whitish spotting except on the chin and over the sternum); from *G. rivicola* (Vences, Glaw & Andreone) and *G. webbi* (Grandison) by its reddish iris colouration (vs. copper and greenish, respectively); from *G. silvanus* (Vences, Glaw & Andreone) by its smaller size (SVL 20.5–25.5 mm vs. 31 mm) and partly whitish vocal sacs (vs. yellowish); from *G. webbi* by femoral glands composed of few large granules (vs. composed of many, small granules) and large inner metatarsal tubercle (vs. small). *Gephyromantis lomorina* sp. n. may be distinguished from *G. klemmeri* by its roughly granular dorsal skin (vs. smooth to shagreened), greenish skin colour (vs. brownish), reddish iris (vs. gold), and strongly protruding inner metatarsal tubercle (vs. small and not protruding).

The call of *G. lomorina* sp. n. may be distinguished from all *Vatomantis* and *Laurentomantis* species in having notes that are clearly pulsed (vs. unpulsed notes in all species except *G. ventrimaculatus*); *Gephyromantis ventrimaculatus* has a higher number of pulses per note notes than *G. lomorina* sp. n. (ca. 6 pulses per note vs. 2–4 in *G. lomorina* sp. n.). The call of *G. lomorina* sp. n. is somewhat similar to that of *G. klemmeri*, especially in having pulsed notes, but the call duration is much longer (1681–1827 ms vs. 626–982 ms), the call has a more distinct amplitude decay (vs. complex amplitude modulation, see Vences et al. 1997), the notes of the call are more homogeneous (vs. distinct components of the call), and it lacks frequency modulation (vs. frequency modulated toward the end of the call).

Description of the holotype. A specimen in a good state of preservation, a piece of tissue taken from the left thigh. SVL 23.3 mm; for other body measurements see Table 1. Body slender. Widest part of head marginally wider than widest part of body. Snout rounded in dorsal and lateral view, protruding slightly over upper jaw in lateral view. Nostrils not distinctly protruding, with lateral openings. Canthus rostralis distinct, concave. Loreal re-

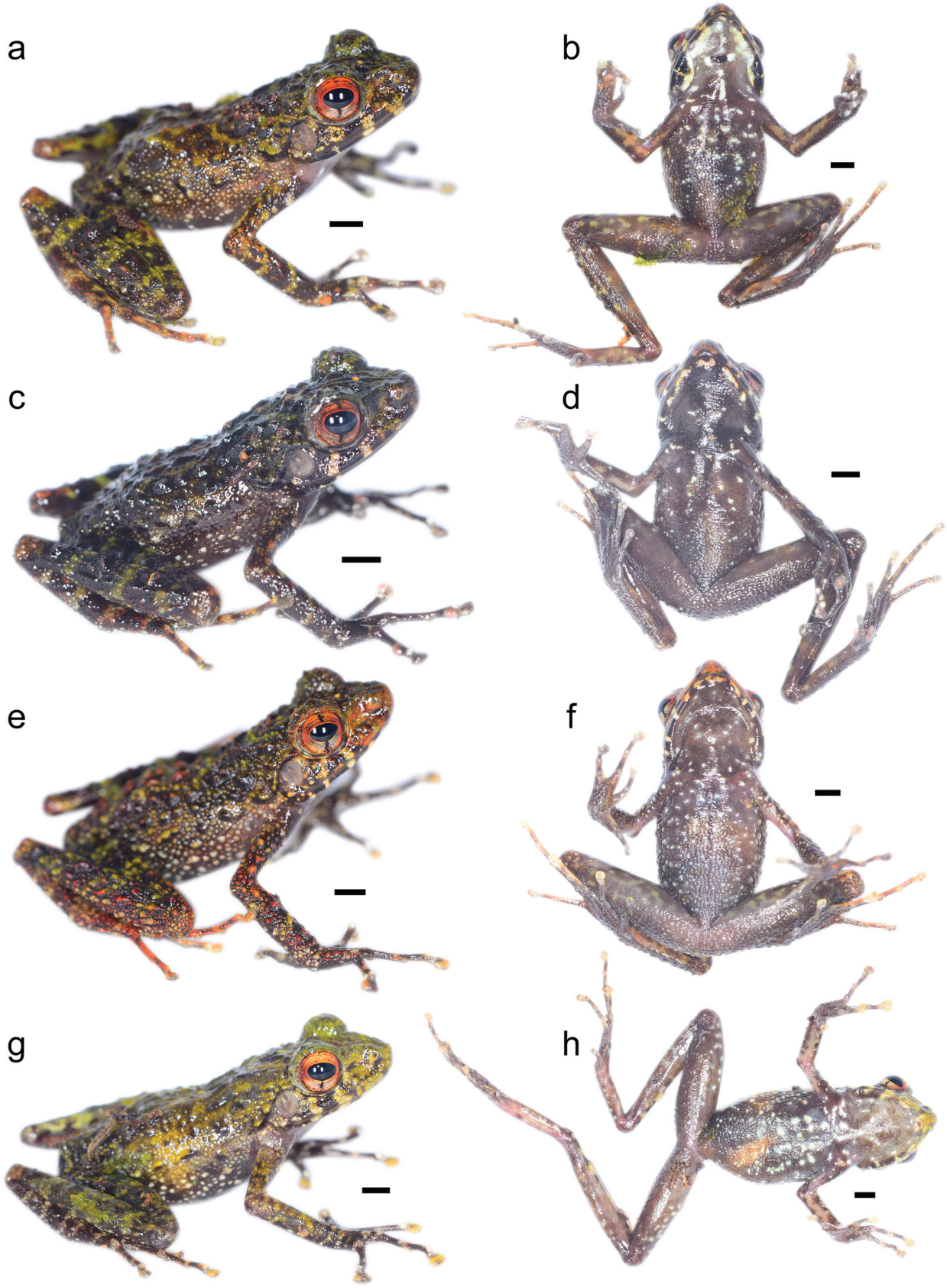

Figure 3. Morphological and chromatic variation among paratypes of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n. from Marojejy in life. **(a–b)** ZSM 420/2016; **(c–d)** UADBA-A 60296; **(e–f)** UADBA-A 60295; and **(g–h)** ZSM 418/2016. Scale bars indicate 2 mm.

gion concave, vertical. Tympanum distinct, fairly small, 53% of eye diameter. Supraocular spines absent. Weakly distinct supratympanic fold running from the eye over the tympanum to above the insertion of the arm. Forelimbs and hindlimbs slender. Inner and outer metacarpal tubercle present, both indistinct. Finger discs enlarged, round. Subarticular tubercles distinct, dark in colour. No webbing between fingers. Comparative finger lengths

Figure 4. Photographs of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n. and its habitat in Sorata. **(a,d)** ZSM 1545/2012; **(b,e)** ZSM 1547/2012; and **(c,f)** ZSM 1549/2012, not to scale; **(g)** habitat where several specimens were found in Sorata, showing **(h,i)** the appearance of the species in situ whilst calling at night.

1 < 2 < 4 < 3, fourth finger much longer than second finger. Toe discs slightly enlarged, smaller than finger discs. Traces of webbing between toes. Comparative toe length 1 < 2 < 3 = 5 < 4. Inner metatarsal tubercle rather large (length about 1.3 mm), protruding strongly distally to resemble a toe. Outer metatarsal tubercle absent. Lateral

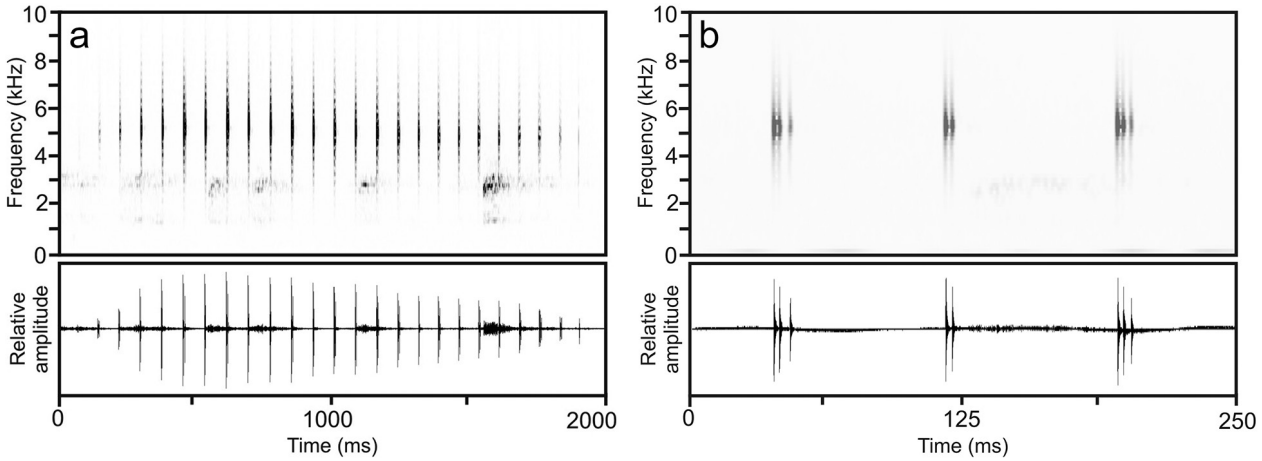

Figure 5. Spectrogram (above) and waveform (below) of a call of the holotype of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n., ZSM 419/2016, from Marojejy. **(a)** A full call (spectrogram shown using FFT of 512 points to visualise call structure); and **(b)** a 250 ms section from the middle of a call, showing the degree of pulsation of each note (spectrogram shown using FFT of 128 points to visualise note structure).

metatarsalia connected. Dorsal skin granular, with numerous small tubercles arranged in mostly parallel lines running posteriorly over the dorsum, with convergent lines of tubercles on the posterior head, and weak rows of tubercles on the hindlimbs and forelimbs. Femoral glands round, consisting of three large granules with an indentation in their middle (similar to type 2 sensu Glaw et al. 2000). Vomerine teeth absent. Maxillary teeth present. Choanae small and lateral. Subgular vocal sacs whitish in distensible portion, blackish on the jaw, fairly small. Tongue bifid, free posteriorly.

Colouration in life (Fig. 2) dorsally mottled with greens, browns, blacks, and yellows. Particularly green over the eyes. Raised ridges on the back were mostly yellowish, but some also with an orange hint. Flanks and lateral head as dorsum. Legs dark brown with yellow-green cross-bands, three on the thigh, three on the shank, and two on the tarsus. The tarsus and dorsal foot were a more ruddy brown than the rest of the body, mottled with a tan orange on the toes and on the heel. A few tubercles on the legs were red. A whitish annulus was present before the terminal disc of each toe and finger. The forelimbs were as the shanks and foot, ruddy brown mottled with yellow-green and dark brown, with a few red tubercles. Whitish spots were present in the inguinal region and the ventral portion of the flank, and also two cream stripes were present below the eye that continued on the bottom lip. The tympanum was distinctly brownish. The venter was umber in base colour with more reddish portions of translucent skin on the ventral side of the arms. The chin had white portions along the lip and especially on the vocal sacs, but the jaw itself was blackish. The venter had distinct white spots. The ventral hindlimbs were umber with irregular pale olive and yellow patches on the ventral thigh and shank. The ventral tarsus, foot, and hand were umber. The femoral glands were fleshy in colour, and the area ventral to the cloaca was pinkish. The iris was copper above and below, and rusty anteriorly and posteriorly, with blackish reticulations and a blackish line above and below the centre of the pupil.

After six months in preservative, the colouration of the holotype has faded to become more uniformly brownish, and areas that were greenish in life have become cream. White areas of the venter are still immaculately white.

Variation. All paratypes resemble the holotype in gross morphology; see Table 1 for morphological variation. Tympanum diameter ranges from 47–79 % of eye, without strong sexual dimorphism in tympanum size. Females are marginally but not significantly larger than males (*t*-test, t = -1.9215, df = 13, $p = 0.07687$). Several paratypes have smaller femoral glands than the holotype. Femoral glands are composed of 2 or 3 large granules (mean 2.875 ± 0.35, n = 8; all but one of eight examined specimens with 3 granules). Females have miniscule raised bumps in the femoral area. There is considerable variation in colouration of the specimens, with some individuals being much darker, and others being more green (Figs 3–4). The chin of females is more solidly dark than that of males, and they lack most white spots. A pair of cream stripes below the eye that continue on the lower lip is present in all specimens. Two specimens (UADBA-A 60299, and ZSM 1545/2012, Fig. 4) have a bright vertebral stripe.

Bioacoustics. Call recordings were made in Marojejy from the holotype ZSM 419/2016 at its collection locality at a distance of 0.5 m during light rain (Suppl. material 1, DOI: 10.7479/nmx8-aq7v). The call is interpreted as an advertisement call as it resembles the advertisement calls of the subgenus *Laurentomantis*, and was emitted without close proximity to other individuals, and while the frog was otherwise inactive (Köhler et al. 2017). Air temperature was not recorded. A strict FFT bandwidth filter was applied to the dataset to remove all sound below 400 Hz in order to remove wind artefacts. Two calls were recorded from the holotype, but numerous calls

were heard whilst searching for this species along the river where it was found. Calls consisted of a rapid series of 24–29 extremely short notes (note duration 6.3 ± 1.9 ms, range 2–10 ms, n = 53; Fig. 5a), each of which had 2.6 ± 0.6 pulses (2–4 pulses, n = 50), the peak amplitudes of which were separated by 2.7 ± 0.6 ms (1–4 ms, n = 53; Fig. 5b). Notes were separated by silent inter-note intervals of 64.6 ± 5.5 ms (47–75 ms, n = 51). The call was amplitude modulated, increasing in amplitude quickly and slowly decaying toward the end of the call. Call duration was 1769–1827 ms (n = 2), with one inter-call interval recorded of 2399 ms. Generally, however, the calls appeared to be emitted rather irregularly. Dominant frequency was 5124–5512 Hz, and the 90 % bandwidth was from 2723–2759 to 6391–6462 Hz.

Similar calls were recorded in Sorata from ZSM 1549/2012 at its collection locality (Suppl. material 2, DOI: 10.7479/nmx8-aq7v). Air temperature was not recorded. The calls strongly resembled those recorded from the holotype. Three calls were recorded, but one was cut off and another had loud calls of *Gephyromantis* (*Duboimantis*) sp. in the background, so only one was analysed. The call consisted of a rapid series of 31 extremely short notes (note duration 6.9 ± 0.8 ms, range 6–10 ms, n = 27 analysed), each of which had 2.0 ± 0.2 pulses (2–3 pulses, n = 27), the peak amplitudes of which were separated by 3.0 ± 0.4 ms (2–4 ms, n = 27). Notes were separated by silent inter-note intervals of 46.3 ± 3.8 ms (41–55 ms, n = 27). The call was amplitude modulated in the same way as that of ZSM 419/2016. Call duration was 1681 ms, and one inter-call interval was ca. 1900 ms. In general however calling was irregular. The dominant frequency was 5555 Hz, and the 90 % bandwidth was from 4979 to 6003 Hz. The call with a loud *Gephyromantis* (*Duboimantis*) sp. in the background was considerably shorter, and consisted of just 11 notes over a duration of 515 ms, but we suppose this call may have been disturbed as it lacked amplitude reduction toward its end.

Distribution. The new species is known from three localities in northeastern Madagascar: (1) Marojejy National Park (type locality), (2) Sorata massif, and (3) Andravory massif (Fig. 6). All specimens were collected between 1164 and 1394 m a.s.l.

Natural history. Specimens were collected near mountain streams in pristine montane riparian rainforest (Fig. 4g). In Marojejy National Park they were encountered during and after light rain, sitting in inconspicuous locations, especially on the fronds of tree ferns, but also on other low vegetation, between a few centimetres and up to 2 m above the ground. Specimens in Sorata were found in similar positions during dry weather, in the days just before the beginning of the rainy season. Males called irregularly and softly (see the call description above). Population density in Marojejy was remarkably high, with around three or four individuals being found along a 10 m stretch of stream. The observed density in Sorata was lower, possibly due to the absence of rain during the observation period. The species occurred in close sympatry with a number of other mantellids, but only few of these (especially *Mantidactylus* aff. *femoralis*) were found in the same microhabitat. Several specimens from Marojejy had pinkish mites (probably of the genus *Endotrombicula*; see Wohltmann et al. 2007) embedded within translucent whitish pustules on the skin of their fingers, toes, and bodies. Nothing is known about the reproduction of this species, but the calling sites suggest an association with lotic water.

Available names. There are no other, earlier names currently available (e.g., junior synonyms) that are assignable to the subgenera *Vatomantis* or *Laurentomantis* and that could apply to the new species.

Etymology. The specific epithet is the Malagasy word *lomorina*, meaning ‘covered in moss’, in reference to the green, mossy appearance of the species in life. It is used as an invariable noun in apposition to the genus name.

Conservation. The species occurs in two regions with very different conservation situations: the highly protected forests of Marojejy National Park, and the unprotected, isolated, and highly threatened forests of Sorata and Andravory. Maminirina et al. (2008) report a study site in the rainforest of Sorata at 970 m a.s.l., but in our surveys in 2012, we detected larger patches of forest only at elevations of ca. 1270 m and above. The new species was collected at lower elevation in Andravory (1164–1179 m a.s.l.), where forest persists. Higher elevation levels of Sorata are covered by high-elevation forests different to those where *G. lomorina* sp. n. was found, and these therefore may not support this species. In this area, the species is therefore directly threatened by the loss of the only forests in which it has been detected.

By contrast in Marojejy, forest extends down to roughly 200 m a.s.l., is highly protected, and the high elevation forest where this species occurs does not seem to be facing any immediate threats. Although the tourist load to Marojejy is relatively high, and the area upslope from the collection locality of the holotype and several paratypes is somewhat polluted with refuse from the nearby tourist camp, the species was abundant around this stream during our survey there in 2016, and presumably inhabits other streams around the same elevation across the massif.

Accommodating this spread of risk is a challenge for the IUCN Red List status. However, *G.* (*V.*) *lomorina* sp. n. is not the first species to have almost exactly this distribution. *Rhombophryne vaventy* Scherz, Ruthensteiner, Vences & Glaw was recently recovered from Sorata (Peloso et al. 2016, Scherz et al. 2016, Lambert et al. 2017) after initially having been described from the same type locality as *G. lomorina* sp. n. (Scherz et al. 2014). In the case of this species, Scherz et al. (2017a) argued for a classification of Endangered under IUCN criterion B1ab(iii), i.e. an extent of occurrence under 5000 km^2 (B1), known from fewer than five

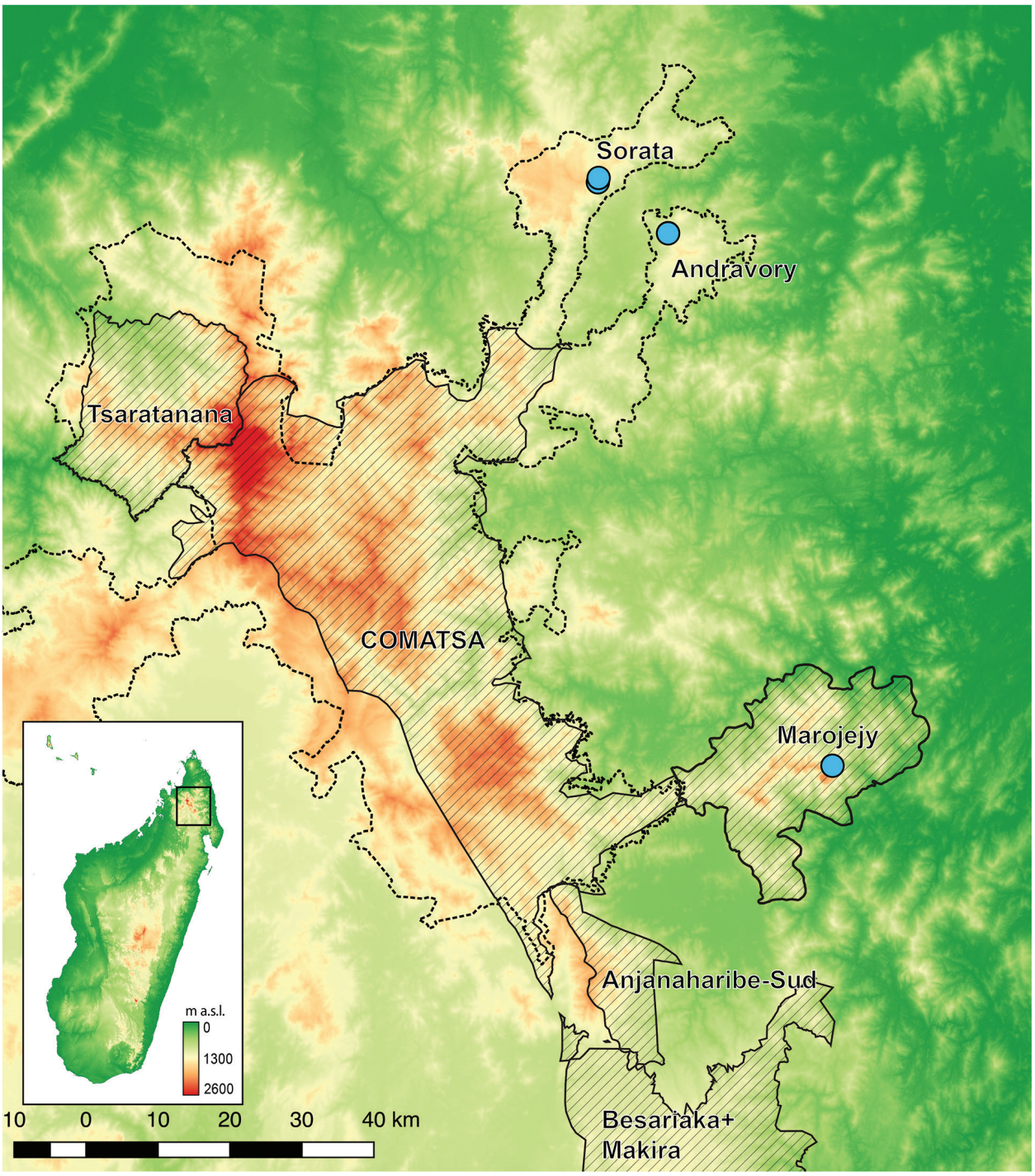

Figure 6. Distribution of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n. in northern Madagascar. Areas with diagonal lines are official protected areas. The dotted outline indicates the proposed area with the scope of the WWF protection plan for this part of Madagascar (Biodev Madagascar Consulting 2014, WWF Madagascar 2015). Three arc second SRTM data from Jarvis et al. (2008).

threat-defined locations (a), and an observed, estimated, inferred, or projected decline (b) in the area, extent, and/or quality of habitat (iii). Given the similar situation in *G. lomorina* sp. n., i.e., very similar, limited distribution and ongoing reduction and threat to a substantial part of its habitat (i.e., the forests of Sorata and Andravory), we propose that the same threat status and justification be given for this species.

Discussion

Gephyromantis (*Vatomantis*) *lomorina* sp. n. is a distinctive species, mostly due to its granular, greenish skin, which is rougher than in all other members of the subgenus *Vatomantis*, but not as rugose as in many species of the subgenus *Laurentomantis*. Indeed, it is in several aspects intermediate between these subgenera, having a

call that sounds similar to both (Vences et al. 2006). Its phylogenetic position is at present basically unresolved between these two subgenera. However, its morphology is clearly more similar to *Vatomantis* than to *Laurentomantis*, as it lacks an outer metatarsal tubercle (present in *Laurentomantis*), has a distinct brown tympanum (less distinct in *Laurentomantis*), lacks a broadened head (usually distinctly broadened in *Laurentomantis*) and has paired subgular vocal sacs (single in *Laurentomantis*) (Glaw and Vences 2006).

Gephyromantis (*Vatomantis*) *rivicola, G.* (*V.*) *silvanus, G.* (*V.*) *lomorina* sp. n., and most *Laurentomantis* species share a unique femoral gland morphology with glands being composed of a small number of large, round granules (each granule representing a single gland within the femoral macrogland; Vences et al. 2007; Fig. 1). Glaw et al. (2000) interpreted these unusual glands as possible intermediate steps between Type 2 glands (sharply delimited groups of numerous granules of up to 0.9 mm diameter) toward Type 3 and 4 glands (a rounded structure composed of few, large granules and an external central depression). The position of *G.* (*V.*) *lomorina* sp. n. appears to make this situation more complicated; formerly, it seemed that granule size had increased and number decreased in *G.* (*V.*) *rivicola* and *G.* (*V.*) *silvanus* while *G.* (*V.*) *webbi* had retained Type 2 glands typical of most other *Gephyromantis* species (Glaw et al. 2000, Vences et al. 2007). However, given the split of *G.* (*V.*) *lomorina* from a more basal node in that clade (Fig. 1), and given the ubiquity of these unusual glands in the sister subgenus *Laurentomantis* (Glaw et al. 2000, Kaffenberger et al. 2012), it seems that Type 2 femoral glands may have independently originated one or more times in this clade. A better resolved phylogeny of the clade will be necessary to better understand the evolution of their femoral gland morphology.

The apparently highly divergent *G.* (*V.*) *lomorina* sp. n. sheds some light on questions regarding the relationships of *G. klemmeri*. Formerly, *G. klemmeri* was considered a member of the subgenus *Gephyromantis*, but Kaffenberger et al. (2012) showed that it has affinities between *Laurentomantis* and *Vatomantis*. They forestalled action on transferring it to one of these subgenera until more data become available, as single genes disagreed as to its position. *Gephyromantis klemmeri* shares femoral gland morphology with both *Laurentomantis* and *Vatomantis*, having large glands with a small number of large granules. This lends credence both to its phylogenetic position being close to these subgenera, and also to the hypothesis that smaller numbers of larger granules in the femoral glands may be ancestral in this clade.

Kaffenberger et al. (2012) suggested three possible alternatives to dealing with the phylogenetic affinities of *G. klemmeri*: (a) including *G. klemmeri* in *Laurentomantis* (its position sister to *Laurentomantis* was supported with 94 % bootstrap support from maximum likelihood and >0.99 posterior probability, but was not supported in maximum parsimony analysis), (b) erecting a new monotypic subgenus, or (c) redefining a more inclusive subgenus *Laurentomantis* that besides *G. klemmeri* would also include *Vatomantis* as a junior synonym (the clade containing *Laurentomantis*, *Vatomantis*, and *G. klemmeri* was supported with 100 % bootstrap support from maximum likelihood, >0.99 posterior probability, and 86 % bootstrap support from maximum parsimony). Determining the best course of taxonomic action will in part depend on the resolution of the phylogenetic relationships of *G. klemmeri* and of *G.* (*V.*) *lomorina* sp. n., in the framework of a more comprehensive revision of *Laurentomantis* and *Vatomantis*, as these subgenera still contain further candidate species requiring in-depth analysis (Vieites et al. 2009).

Gephyromantis (*Vatomantis*) *lomorina* sp. n. also sheds light on the biogeography of northern Madagascar, providing yet more evidence for a strong link between Sorata and Marojejy. The environmental conditions of these two regions are similar (Brown et al. 2016), and various species originally described from one of the two areas have subsequently been discovered in the other, e.g. *Rhombophryne vaventy* (Peloso et al. 2016, Scherz et al. 2016, 2017a, Lambert et al. 2017), *Gephyromantis* (*Asperomantis*) *tahotra* (Glaw et al. 2011, Vences et al. 2017), and *G.* (*D.*) *schilfi* (Glaw and Vences 2000, Scherz et al. 2017b). These similarities are generally limited to species found above 1200 m, probably because forest below 1200 m in Sorata has been mostly eradicated.

We predict that similarities between faunal compositions of the mountainous massifs of northern Madagascar are limited by elevational connectivity. For instance, there is continued connectivity between regions of elevation up to 1400 m from Sorata to Marojejy and indeed roughly to the Manongarivo massif as well. There is no connectivity above this elevation however; areas of over 1400 m across the different massifs are separated by lower elevations, leading to island-like isolation of peak areas. Therefore, we predict that species occurring above 1400 m will show a greater degree of microendemism, and those below this elevation will have a greater probability of occurring more widely; the higher a species' centre of elevational distribution is located, the greater its chance of being microendemic. No absolute threshold of turnover is expected, because major climate fluctuations in the past will likely have blurred elevational boundaries over time.

So far, evidence appears to support this hypothesis; as already stated, several species from around 1300 m are shared between Marojejy and Sorata (and Andravory, though at present only limited and generally unpublished data are available from this forest), and some species known from higher elevations are so far thought to be microendemic to either region, e.g. *Rhombophryne longicrus* (Scherz et al. 2015), *Gephyromantis* (*Duboimantis*) *tohatra* (Scherz et al. 2017b), *Calumma jejy*, and *C. peyrierasi*. Assuming this hypothesis is correct, it raises questions about species that are microendemic at lower elevations, but opportunities to study and understand these taxa are increasingly limited by the fact that forest at lower elevations is disappearing outside of protected

areas. Conservation efforts must be redoubled to ensure that these study systems may remain long enough to be investigated and understood.

Acknowledgements

As always, we are grateful to the Malagasy authorities of the Ministry of Environments and Forests for providing us with permits. Field research was conducted under permit N° 215/16/MEEF/SG/DGF/DSAP/SCB.Re (dated 5 September 2016) and N° 265/12/MEF/SG/DGF/DCB.SAP/SCB (dated 18 October 2012). Specimens were exported under permits N° 010N-EA01/MG17 (dated 4 January 2017) and N° 163N-EA12/MG12 (dated 17 December 2012). This work was carried out in collaboration with the Mention Zoologie et Biodiversité Animale, Universite d'Antananarivo, to whom we are also grateful for the loan of the paratype series. We are also grateful to R. Walker, W.-Y. Crawley, T. H. Rafeliarisoa, and the Andravory team for their help in Andravory, and A. Razafimanantsoa and T. Rajoafiarison for their help in Marojejy and Sorata. AR and MCB were supported by fellowships of the Deutscher Akademischer Austauschdienst. MV and MDS were supported by grants of the Deutsche Forschungsgemeinschaft (VE247/13-1 and 15-1). The fieldwork of OH, FG, AR, and FR was supported by the Mohamed bin Zayed Species Conservation Fund (project 11253064). The publication of this article in Zoosystematics and Evolution was made possible by the Museum für Naturkunde Berlin.

References

Biodev Madagascar Consulting (2014) Document de référence sur la NAP complexe Ambohimirahavavy Marivorahona en vue de l'evaluation environnementale par le CTE. Unpublished report. Accessed 14 June 2017. Available from: https://goo.gl/4KgD9W [Archived by WebCite® at http://www.webcitation.org/6saYQDhEv]

Brown JL, Sillero N, Glaw F, Bora P, Vieites DR, Vences M (2016) Spatial biodiversity patterns of Madagascar's amphibians and reptiles. PLoS One 11(1): e0144076. https://doi.org/10.1371/journal.pone.0144076

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Glaw F, Hoegg S, Vences M (2006) Discovery of a new basal relict lineage of Madagascan frogs and its implications for mantellid evolution. Zootaxa 1334: 27–43.

Glaw F, Köhler J, Vences M (2011) New species of *Gephyromantis* from Marojejy National Park, northeast Madagascar. Journal of Herpetology 45(2): 155–160. https://doi.org/10.1670/10-058.1

Glaw F, Vences M (2000) A new species of *Mantidactylus* from northeastern Madagascar (Amphibia, Anura, Ranidae) with resurrection of *Mantidactylus blanci* (Guibé, 1974). Spixiana 23(1): 71–83.

Glaw F, Vences M (2001) Two new sibling species of *Mantidactylus cornutus* from Madagascar. Spixiana 24(2): 177–190.

Glaw F, Vences M (2006) Phylogeny and genus-level classification of mantellid frogs (Amphibia, Anura). Organisms Diversity & Evolution 6(3): 236–253. https://doi.org/10.1016/j.ode.2005.12.001

Glaw F, Vences M, Gossmann V (2000) A new species of *Mantidactylus* (subgenus *Guibemantis*) from Madagascar, with a comparative survey of internal femoral gland structure in the genus (Amphibia: Ranidae: Mantellinae). Journal of Natural History 34: 1135–1154. https://doi.org/10.1080/00222930050020140

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4, International Centre for Tropical Agriculture (CIAT). Available from: http://srtm.csi.cgiar.org.

Kaffenberger N, Wollenberg KC, Köhler J, Glaw F, Vieites DR, Vences M (2012) Molecular phylogeny and biogeography of Malagasy frogs of the genus *Gephyromantis*. Molecular Phylogenetics and Evolution 62(1): 555–560. https://doi.org/10.1016/j.ympev.2011.09.023

Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, Glaw F, Haddad CFB, Rödel M-O, Vences M (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. Zootaxa 4251(1): 1–124. https://doi.org/10.11646/zotaxa.4251.1.1

Köhler J, Vieites DR, Bonett RM, García FH, Glaw F, Steinke D, Vences M (2005) New amphibians and global conservation: a boost in species discoveries in a highly endangered vertebrate group. BioScience 55(8): 693–696. https://doi.org/10.1641/0006-3568(2005)055[0693:NAAGCA]2.0.CO;2

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lambert SM, Hutter CR, Scherz MD (2017) Diamond in the rough: a new species of fossorial diamond frog (*Rhombophryne*) from Ranomafana National Park, southeastern Madagascar. Zoosystematics and Evolution 93(1): 143–155. https://doi.org/10.3897/zse.93.10188

Maminirina CP, Goodman SM, Raxworthy CJ (2008) Les micro-mammifères (Mammalia, Rodentia, Afrosoricida et Soricomorpha) du massif du Tsaratanana et biogéographie des forêts de montagne de Madagascar. Zoosystema 30: 695–721.

Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR, Version 2.0. Privately published, University of Hawaii.

Peloso PLV, Frost DR, Richards SJ, Rodrigues MT, Donnellan S, Matsui M, Raxworthy CJ, Biju SD, Lemmon EM, Lemmon AR, Wheeler WC (2016) The impact of anchored phylogenomics and taxon sampling on phylogenetic inference in narrow-mouthed frogs (Anura, Microhylidae). Cladistics 32(2): 113–140. https://doi.org/10.1111/cla.12118

Perl RGB, Nagy ZT, Sonet G, Glaw F, Wollenberg KC, Vences M (2014) DNA barcoding Madagascar's amphibian fauna. Amphibia-Reptilia 35: 197–206. https://doi.org/10.1163/15685381-00002942

Rambaut A, Drummond AJ (2007) Tracer v1.5. Available from: http://beast.bio.ed.ac.uk/Tracer.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sabino-Pinto J, Mayer CJ, Meilink WRM, Grasso D, Raajmakers CCB, Russo VG, Segal M, Stegen G, Clegg J, Srikanthan AN, Glaw F, Vences M (2014) Descriptions of the advertisement calls of three sympatric frog species in the subgenus *Vatomantis* (genus *Gephyromantis*) from Madagascar. Herpetology Notes 7: 67–73.

Scherz MD, Hawlitschek O, Andreone F, Rakotoarison A, Vences M, Glaw F (2017a) A review of the taxonomy and osteology of the *Rhombophryne serratopalpebrosa* species group (Anura: Microhylidae) from Madagascar, with comments on the value of volume rendering of micro-CT data to taxonomists. Zootaxa 4273(3): 301–340. https://doi.org/10.11646/zootaxa.4273.3.1

Scherz MD, Rakotoarison A, Hawlitschek O, Vences M, Glaw F (2015) Leaping towards a saltatorial lifestyle? An unusually long-legged new species of *Rhombophryne* (Anura, Microhylidae) from the Sorata massif in northern Madagascar. Zoosystematics and Evolution 91(2): 105–114. https://doi.org/10.3897/zse.91.4979

Scherz MD, Razafindraibe JH, Rakotoarison A, Bletz MC, Glaw F, Vences M (2017b) Yet another small brown frog from high altitude on the Marojejy Massif, northeastern Madagascar. Zootaxa 4347(3): 572–582. https://doi.org/10.11646/zootaxa.4347.3.9

Scherz MD, Ruthensteiner B, Vences M, Glaw F (2014) A new microhylid frog, genus *Rhombophryne*, from northeastern Madagascar, and a re-description of *R. serratopalpebrosa* using micro-computed tomography. Zootaxa 3860(6): 547–560. https://doi.org/10.11646/zootaxa.3860.6.3

Scherz MD, Vences M, Rakotoarison A, Andreone F, Köhler J, Glaw F, Crottini A (2016) Reconciling molecular phylogeny, morphological divergence and classification of Madagascan narrow-mouthed frogs (Amphibia: Microhylidae). Molecular Phylogenetics and Evolution 100: 372–381. https://doi.org/10.1016/j.ympev.2016.04.019

Vallan D, Glaw F, Andreone F, Cadle JE (1998) A new treefrog species of the genus *Boophis* (Anura: Ranidae: Rhacophorinae) with dermal fringes from Madagascar. Amphibia-Reptilia 19(4): 357–368. https://doi.org/10.1163/156853898X00025

Vences M, Glaw F, Andreone F (1997) Description of two new frogs of the genus *Mantidactylus* from Madagascar, with notes on *Mantidactylus klemmeri* (Guibe, 1974) and *Mantidactylus webbi* (Grandison, 1953) (Amphibia, Ranidae, Mantellinae). Alytes 14(4): 130–146.

Vences M, Glaw F, Andreone F, Jesu R, Schimmenti G (2002) Systematic revision of the enigmatic Malagasy broad-headed frogs (*Laurentomantis* Dubois, 1980), and their phylogenetic position within the endemic mantellid radiation of Madagascar. Contributions to Zoology 70(4): 191–212.

Vences M, Glaw F, Marquez R (2006) The Calls of the Frogs of Madagascar. 3 Audio CD's and booklet. Fonoteca Zoológica, Madrid, Spain, 44 pp.

Vences M, Köhler J, Pabijan M, Bletz M, Gehring P-S, Hawlitschek O, Rakotoarison A, Ratsoavina FM, Andreone F, Crottini A, Glaw F (2017) Taxonomy and geographic distribution of Malagasy frogs of the *Gephyromantis asper* clade, with description of a new subgenus and revalidation of *Gephyromantis ceratophrys*. Salamandra 53(1): 77–98.

Vences M, Lyra ML, Perl BRG, Bletz MC, Stankovic D, Geffers R, Haddad CFB, Steinfartz S, Martins Lopes C, Jarek M, Bhuju S (2016) Freshwater vertebrate metabarcoding on Illumina platforms using double-indexed primers of the mitochondrial 16S rRNA gene. Conservation Genetics Resources 8(1): 1–5. https://doi.org/10.1007/s12686-016-0550-y

Vences M, Raxworthy CJ, Nussbaum RA, Glaw F (2003) A revision of the *Scaphiophryne marmorata* complex of marbled toads from Madagascar, including the description of a new species. Herpetological Journal 13: 69–79.

Vences M, Wahl-Boos G, Hoegg S, Glaw F, Oliveira ES, Meyer A, Perry S (2007) Molecular systematics of mantelline frogs from Madagascar and the evolution of their femoral glands. Biological Journal of the Linnean Society 92(2007): 529–539.

Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences of the USA 106(20): 8267–8272. https://doi.org/10.1073/pnas.0810821106

Vieites DR, Wollenberg KC, Vences M (2012) Not all little brown frogs are the same: a new species of secretive and cryptic *Gephyromantis* (Anura: Mantellidae) from Madagascar. Zootaxa 3344: 34–46.

Wohltmann A, du Preez L, Rödel M-O, Köhler J, Vences M (2007) Endoparasitic mites of the genus *Endotrombicula* Ewing, 1931 (Acari: Prostigmata: Parasitengona: Trombiculidae) from African and Madagascan anurans, with description of a new species. 54: 225–235. https://doi.org/10.14411/fp.2007.031

WWF Madagascar (2015) Plan d'Aménagement et de gestion intégré du complexe d'aires protegées Ambohimirahavavy Marivorahona, Report Draft. Accessed 14 June 2017. Available from goo.gl/GGXP2D

Supplementary material 1

Advertisement call of *Gephyromantis lomorina* sp. n.

Authors: Mark D. Scherz, Oliver Hawlitschek, Jary H. Razafindraibe, Steven Megson, Fanomezana Mihaja Ratsoavina, Andolalao Rakotoarison, Molly C. Bletz, Frank Glaw, Miguel Vences

Data type: WAV File (.wav)

Explanation note: Call recording of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n. ZSM 419/2016 (ZCMV 15221). Calls recorded at 21h20 on 18 November 2016 near Camp Simpona (ca. 14.4366°S, ca. 49.7434°E, ca. 1325 m a.s.l.) in Marojejy National Park, Sava Region, Antsiranana Province, northeastern Madagascar, by M. D. Scherz. Frog was ca. 1 m above the ground on a fern near a small river, calling occasionally during light rain. Air temperature was not taken. Recording distance was 0.5 m. Animal Sound Archive: https://doi.org/10.7479/nmx8-aq7v.

Link: https://doi.org/10.3897/zse.94.21037.suppl1

Supplementary material 2

Advertisement call of *Gephyromantis lomorina* sp. n.

Authors: Mark D. Scherz, Oliver Hawlitschek, Jary H. Razafindraibe, Steven Megson, Fanomezana Mihaja Ratsoavina, Andolalao Rakotoarison, Molly C. Bletz, Frank Glaw, Miguel Vences

Data type: WAV File (.wav)

Explanation note: Call recording of *Gephyromantis* (*Vatomantis*) *lomorina* sp. n. ZSM 1549/2012 (FGZC 3714). Calls recorded at night on 30 November 2012 on the Sorata massif (creek near campsite, 13.6829°S, 49.4403°E, 1325 m a.s.l.), Sava Region, Antsiranana Province, northeastern Madagascar, by O. Hawlitschek. Ecological data not available. Air temperature and recording distance were not noted. Animal Sound Archive: https://doi.org/10.7479/nmx8-aq7v.

Link: https://doi.org/10.3897/zse.94.21037.suppl2